

## Larvae of Nearshore Fishes in Oceanic Waters of the Central Equatorial Pacific<sup>1</sup>

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**ABSTRACT:** Larvae of 72 taxa of nearshore fishes were identified from mid-water trawl samples taken in oceanic waters between Hawai'i and Tahiti. Catches of nearshore fish larvae and number of taxa caught declined with distance from the closest island. Most of the taxa were taken only within 300 km of the nearest island; only eight taxa were taken more than twice at greater distances. Highest catches were at stations close to major island groups, the Hawaiian or Society islands. Among stations closest to small isolated islands, densities were higher relative to distance from shore within the North Equatorial Countercurrent and the Equatorial Undercurrent; these strong eastward-flowing currents routinely transport larvae > 1000 km from likely sources upstream. Even in the zones of higher abundance, densities of nearshore larvae were much lower than in coastal waters, and adequate sampling in oceanic waters requires larger, faster nets than those typically used for ichthyoplankton studies.

THE RELATIVE ABILITIES of different taxa of nearshore fishes to disperse across oceanic barriers are for the most part inferred from knowledge of larval life span and adult distribution (e.g., Brothers and Thresher 1985, Victor 1986). There are few data on occurrence of larvae or juveniles of nearshore species at distances well removed from the nearest shallow-water sources. Richards's (1984) data indicated that some nearshore fish larvae occurred several hundred kilometers from land in the Caribbean, and Hare and Cowen (1991) documented transport of labrid larvae over distances of 600–700 km along the coast of the eastern United States via the Gulf Stream and warm-core rings. Data from truly oceanic areas, well removed from continents or large islands, are much fewer. Leis (1983, 1984) and Victor (1987) reported off-shore captures of nearshore larvae (mostly labrids) in the eastern Pacific and discussed

their occurrence relative to larval life spans and estimated velocities of prevailing currents.

In this paper I present data on nearshore fish larvae taken in a series of oceanic mid-water trawl collections in the central equatorial Pacific between Hawai'i and Tahiti. Though the sampling program was originally designed to investigate distribution of small oceanic fishes, the sample locations ranged between 24 and almost 1200 km from the closest nearshore habitat. The samples were taken with a large net, and the volume filtered at each station was considerably larger than that of plankton tows taken by most previous studies. The primary purpose of this report is to document the types and frequency of nearshore larvae as a function of distance from shore and to consider the role of prevailing currents and other physical processes in larval dispersal.

<sup>1</sup> Sample collection and rough sorting were supported by NSF OCE77-09202 and the remainder of the analyses by the University of Hawai'i, Hawai'i Institute of Marine Biology. Manuscript accepted 15 May 1994.

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### MATERIALS AND METHODS

Samples examined were taken on a series of cruises between Hawai'i and Tahiti during

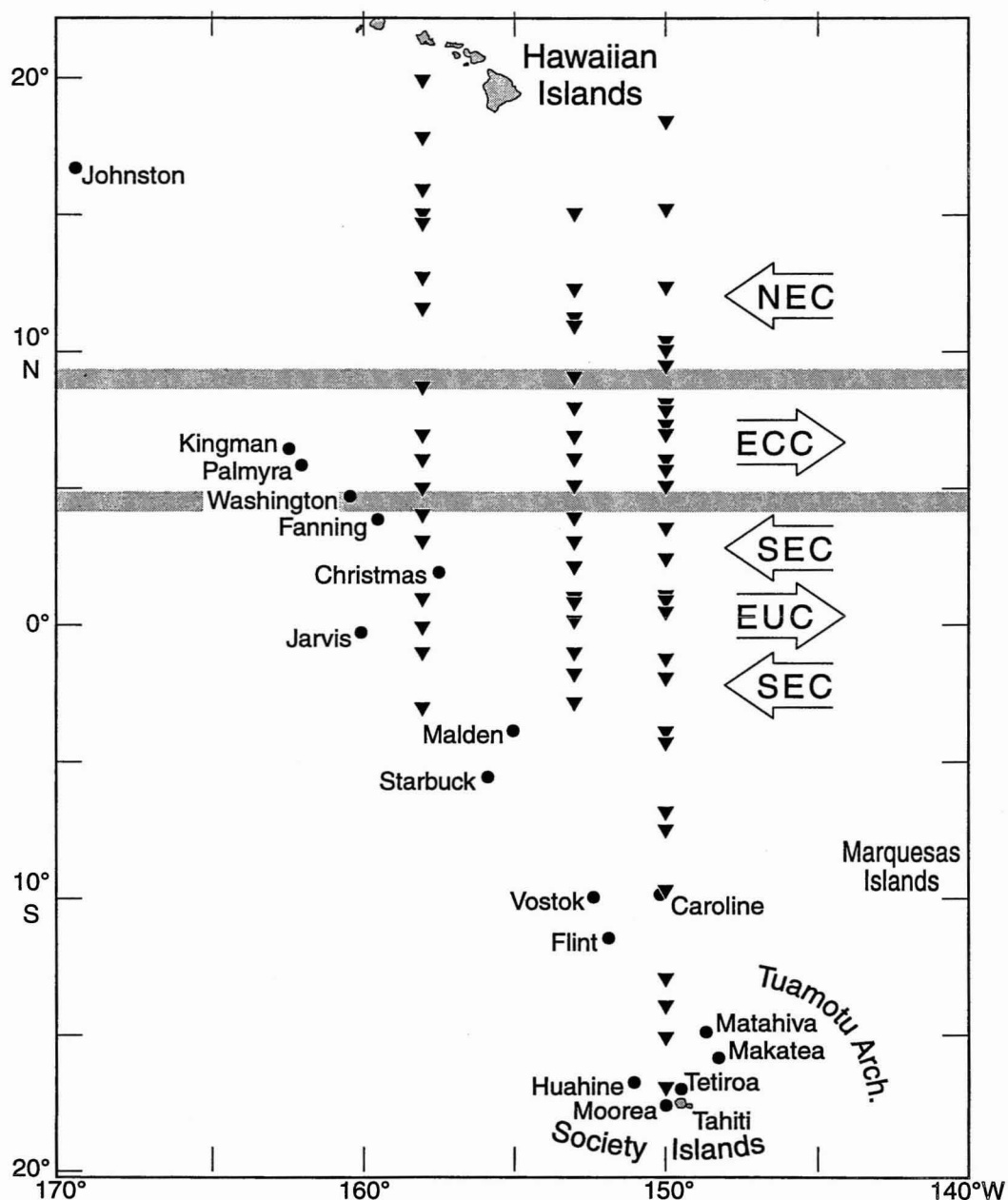


FIGURE 1. Map of the central Pacific between Hawai'i and Tahiti showing locations of 71 nighttime midwater trawl samples (triangles) and of relevant islands. Small islands are indicated by solid circles. For the Society and Tuamotu islands, only the individual islands closest to the stations are shown. Because of their distance from the samples, several islands in the southwest corner of the map are omitted. Broad shaded lines show the approximate boundaries between the North Equatorial Current (NEC), North Equatorial Countercurrent (ECC), and South Equatorial Current (SEC). Arrows indicate the direction of these currents and of the Equatorial Undercurrent (EUC).

1977–1980. The sampling program and procedures were given in Clarke (1987) and are briefly summarized here. Oblique tows with a 3-m Isaacs-Kidd midwater trawl lined with ca. 6-mm (1/4-inch) mesh and with a 1-m diameter cod end of 0.333-mm mesh were taken at ca. 1° intervals of latitude between 20° N and 4° S along 153° W and 158° W and between 20° N and 18° S along 150° W (Figure 1). The zone between 5 and 8° N, 150° W was sampled on five different cruises, and four other stations were sampled twice during the program. Seventy-one samples were taken at night between the surface and 300–400 m; the volume sampled in the upper 100 m, where most nearshore larvae probably occur (Leis 1991), was 20,000–40,000 m<sup>3</sup> per tow. Twenty-nine other samples, mostly taken during the day, fished to greater depths and were lowered and raised rapidly through the upper 300 m thus sampling smaller volumes in the upper 100 m (<10,000 m<sup>3</sup> per tow). Unless explicitly noted, the results and discussion refer only to the 71 night tows.

Fish larvae and juveniles from the samples were sorted using a 3× magnifier; previous experience had shown that ca. 90% of the larvae under 3–5 mm and all larger larvae were recovered by this procedure. Larvae of oceanic taxa were separated, and all larvae of nearshore or potentially nearshore taxa were identified to at least family and to lower taxonomic levels if possible. Notochord or standard length was measured to the nearest 0.1 mm. Because I usually was not certain how many species were included in identifications to genus, I have dispensed with the customary “sp.” or “spp.” after generic names. Distinct forms of certain families (mainly labrids) that could not be definitely identified to genus are identified as “Labrid T,” etc. These designations are identical with those in Clarke (1991), where tentative generic identifications are given. The distances along a great circle arc between each sample and the nearest island were calculated from the latitudes and longitudes of the stations and the islands. Locations and directions of prevailing currents in the study area were based on Wyrtki and Kilonsky (1992).

## RESULTS AND DISCUSSION

A total of 392 larvae or small juveniles of nearshore or potentially nearshore taxa was found in the samples (Table 1); all but 12 were from night tows. Those of the ostraciid *Lactoria diaphana* (Bloch & Schneider) ( $n = 5$ ) were excluded from further analyses. All were taken >500 km from the nearest island, and *L. diaphana* is known to mature and spawn pelagically (Leis and Moyer 1985). Larvae of certain other taxa could also have originated from pelagic spawning. The Echineidae and some of the Tetraodontiformes may have included species that spawn pelagically. *Zenion* and the carangid genus *Decapturus* are coastal pelagic as adults, but could occasionally spawn at considerable distances from shore. The congrid leptocephali could include deep benthic species that originated from seamounts or the ocean floor. None of these taxa were, however, taken frequently, and their inclusion had little effect on the overall results. The frequently captured *Ectreposebastes*, which may also spawn offshore, is considered below.

There was a general decline in frequency of capture of nearshore larvae, mean numbers per tow, and number of taxa with distance from the nearest island (Table 2). The greatest decline occurred between 200 and 300 km distance; consequently, captures within 300 km were considered “inshore” and those at >300 km, “offshore.” Other studies have suggested that nearshore fish larvae decline rapidly in abundance and diversity a few hundred kilometers from the nearest shore. Leis (1984) noted that nearshore fish larvae were very rarely taken >500 km offshore of the Central American coast, and Fedoryako (1989) reported that “coastal” larvae in the “upper epipelagial” declined most rapidly at distances of 100–300 km from shore in the Pacific and 300–600 km from shore in the Indian Ocean.

Catches were, however, obviously influenced by factors other than distance from shore. The three highest catches were from stations close to major groups of high islands. One (17° S, 150° W; 34 larvae) was

TABLE 1

LIST OF LARVAL FISH TAXA COLLECTED, NUMBER OF SPECIMENS AND THEIR SIZE RANGE, AND RANGE OF DISTANCES BETWEEN COLLECTION SITES AND NEAREST NEARSHORE HABITAT FOR 71 NIGHTTIME AND 29 OTHER TRAWL SAMPLES TAKEN IN THE CENTRAL EQUATORIAL PACIFIC

TAXON	NO. (SIZE IN mm)	DISTANCE (km)
Muraenidae	13 (34–65)	24–786
Nettastomatidae	1 (97)	272
Ophichthidae	1 (18)	44
Chlopsidae	4 (59–60)	44–181
Muraenosocidae	1 (59)	335
Congridae		
Congrinae	11 (60–162)	44–272 + 525
Bathymyrinae	5 (240–307)	236–800
Synodontidae		
<i>Trachinocephalus</i>	1 (34)	24
<i>Synodus</i>	7 (20–32)	140
Ophidiidae	1 (12)	468
<i>Brotula</i>	1 (7)	140
Holocentridae		
Holocentrinae	4 (4–8)	44–993
Myripristinae	4 (3–7)	44–285
Macrurocyttidae		
<i>Zenion</i>	1 (24)	272
Fistulariidae		
<i>Fistularia</i>	2 (84–86)	44–140
Scorpaenidae		
Scorpaeninae	5 (6–12)	140–272 + 987
<i>Scorpaenodes</i>	1 (8)	140
<i>Ectreposebastes</i>	20 (4–28)	158–932
<i>Setarches</i>	2 (10–29)	44–202
Acropomatidae		
<i>Synagrops</i>	7 (4–26)	158–987
Apogonidae		
Apogoninae	5 (4–25)	44–223 + 522
Carangidae	4 (3–11)	35–295 + 1,131
<i>Decapturus</i>	5 (3–20)	44–631
Chaetodontidae	3 (5–12)	35–525
Cirrhitidae	3 (6–22)	23–469
Lutjanidae	2 (9–10)	35–158
Caesionidae	1 (9)	202
Lethrinidae	1 (23)	993
Mullidae	5 (11–20)	740–1,131
Pomacanthidae	8 (7–16)	44–272 + 496
Priacanthidae	1 (9)	272
Serranidae		
Epinephelinae	1 (16)	994
Anthiinae	47 (3–25)	24–664
<i>Luzonichthys</i>	41 (3–29)	35–495
Pseudogrammididae	7 (9–14)	223–800
Callanthiidae		
<i>Grammatonotus</i>	3 (23–27)	134–254
Symphysanodontidae		
<i>Symphysanodon</i>	2 (5–45)	35–272
Echeneididae	2 (9–21)	479–987
Labridae	1 (4)	158
Labrid 3	1 (13)	140
Labrid S	16 (6–7)	140–172
Labrid B	1 (6)	158

TABLE 1 (continued)

TAXON	NO. (SIZE IN mm)	DISTANCE (km)
Labrid N	2 (3-9)	140-920
Labrid E	1 (22)	140
Labrid T	18 (5-17)	24-987
Labrid O	1 (15)	140
Labrid G	1 (12)	140
Pomacentridae	2 (7-9)	35-223
<i>Chromis</i>	11 (7-16)	134-987
Scaridae		
Scarinae	4 (3-7)	44-158
Calotominae	1 (13)	140
Acanthuridae	4 (2-4)	44-285
<i>Acanthurus</i>	12 (5-11)	35-920
<i>Naso</i>	6 (8-30)	147-522 + 909
<i>Ctenochaetus</i>	3 (6-8)	44-994
Percophididae		
<i>Chrionema</i>	1 (16)	181
Pinguipididae		
<i>Parapercis</i>	9 (4-6)	140-272
Blenniidae		
Salariaiini	7 (4-19)	44-285
<i>Plagiotremus</i>	1 (26)	740
Ammodytidae	3 (10-15)	140-596
Eleotridae	4 (5-7)	140
Gobiidae	7 (5-16)	134-294
Microdesmidae	6 (6-14)	158-285
Callionymidae	2 (4)	140-920
Balistidae	1 (5)	1,140
Tetraodontidae	1 (21)	140
Diodontidae	1 (15)	484
Ostraciidae		
<i>Lactoria diaphana</i> (Bloch & Schneider)	5 (7-18)	517-994
<i>Lactoria fornasini</i> (Bianconi)	1 (7)	140
Bothidae		
<i>Bothus</i>	6 (13-34)	117-555
<i>Engyprosopon</i>	16 (5-18)	140-272
<i>Pelecanichthys</i>	1 (138)	522
Soleidae	1 (28)	140
Cynoglossidae	1 (17)	44

only 44 km away from the small island of Tetiaroa and almost as close to the larger islands of Moorea and Tahiti in the Society Islands. Stations at 19.9° N (96 larvae) and 17.8° N (25 larvae) along 158° W were 141 and 272 km, respectively, away from the nearest point in the Hawaiian Islands—and >1200 km from Johnston Atoll, the next nearest island. These catches are comparable with those reported by Clarke (1991) for similar samples taken much closer to shore in Hawai'i. The two stations were almost directly west of the island of Hawai'i, where

mesoscale eddies are frequently generated and eventually spun off downstream (Patzert 1969). Lobel and Robinson (1988) considered the role of these eddies in entraining larvae and returning them to nearshore habitats. The high catches reported here could mean that considerable numbers of entrained nearshore larvae are also carried well offshore by eddies that move downstream from the area where they were generated.

Inspection of the data from the remaining 68 night tows, all of which were closest to small isolated islands, indicated that stations

TABLE 2

SUMMARY OF CATCH DATA FOR NEARSHORE FISH LARVAE FROM 71 NIGHTTIME MIDWATER TRAWL TOWS IN THE CENTRAL EQUATORIAL PACIFIC

DISTANCE (km)	NO. TOWS (+TOWS)	MEAN LARVAE PER TOW (RANGE, +TOWS)	MEAN NO. TAXA PER TOW
0-100	3 (3)	21.3 (8-32)	11.7
101-200	8 (7)	20.6 (4-96)	8.0
201-300	8 (8)	8.4 (2-25)	5.4
301-400	5 (4)	2.6 (1-8)	2.2
401-500	7 (6)	2.0 (1-6)	1.9
501-600	9 (7)	1.8 (1-5)	1.6
601-700	4 (3)	2.0 (1-5)	1.0
701-800	7 (4)	0.9 (1-2)	0.9
801-900	5 (3)	1.0 (1-3)	1.0
901-1,000	9 (4)	1.3 (1-5)	1.2
1,001-1,200	6 (2)	0.8 (1-4)	0.5

NOTE: Given for each 100-km increment of distance from nearest nearshore habitat are number of tows, number of positive tows (+tows), mean number of larvae per tow, range for positive tows only, and mean number of larval taxa (see Table 1) per tow.

at 5-8° N and 2° S-2° N tended to have higher catches, relative to distance from the nearest island, than those from other latitudes (Figure 2). This tendency was in part because 5-8° N, 150° W was sampled repeatedly during the survey, and thus a disproportionate share of the stations was from that zone. Nevertheless, densities of larvae were slightly higher in both the latitudinal zones mentioned above. Assuming that ca. 30,000 m<sup>3</sup> was filtered in the upper 100 m per tow, densities for stations > 300 km from the nearest island were ca. 0.5/10<sup>4</sup> m<sup>3</sup> for 5-8° N and 0.7/10<sup>4</sup> m<sup>3</sup> for 2° S-2° N as compared with ca. 0.3/10<sup>4</sup> m<sup>3</sup> for offshore stations at other latitudes. The highest catch of the day tows, four larvae, was at 5.9° N, 150° W, and three of the four specimens of "*Thalassoma*" larvae (apparently the same as my Labrid T) reported by Leis (1983) were from 5-8° N, 151° W.

Both of these zones of higher abundance lie within strong eastward-flowing currents (Figure 1). The North Equatorial Counter-current (ECC) is centered at ca. 6-7° N, and the Equatorial Undercurrent (EUC) is centered on the equator. Though most of the stations at 5-8° N were closest to Christmas Island, the latter lies south of the ECC in the westward-flowing South Equatorial Current (SEC) and is downstream of most of the sta-

tions. Transport to 5-8° N from Christmas would require northward transport in an area where currents are predominately east-west and subsequent entrainment in the ECC. The more likely sources for larvae at 5-8° N were Palmyra Island and Kingman Reef, which were farther away than Christmas but directly upstream in the ECC. Similarly, the stations at 2° S-2° N were closest to either Christmas or Malden islands. The former is at the northern edge of the EUC and the latter well south of it, and flow in the upper 100 m is either mostly or exclusively westward in the SEC. The more likely source for larvae near the equator was probably Jarvis Island, which is located upstream nearly in the center of the EUC. Though the surface waters at Jarvis also flow west in the SEC, the stronger EUC is centered at ca. 100 m and extends very close to the surface. Leis (1984) suggested that the EUC might be too cool for larvae of shallow-water fishes, but in fact temperatures in the upper 100 m of the EUC are only 1-2°C lower than in the surrounding waters of the SEC.

Most of the 72 taxa in Table 1 were only taken close to islands; 21 were taken only at one or two of the three stations close to large island groups: the two stations west of Hawai'i and the one near Tahiti. Seven other taxa were taken only within 200 km of the

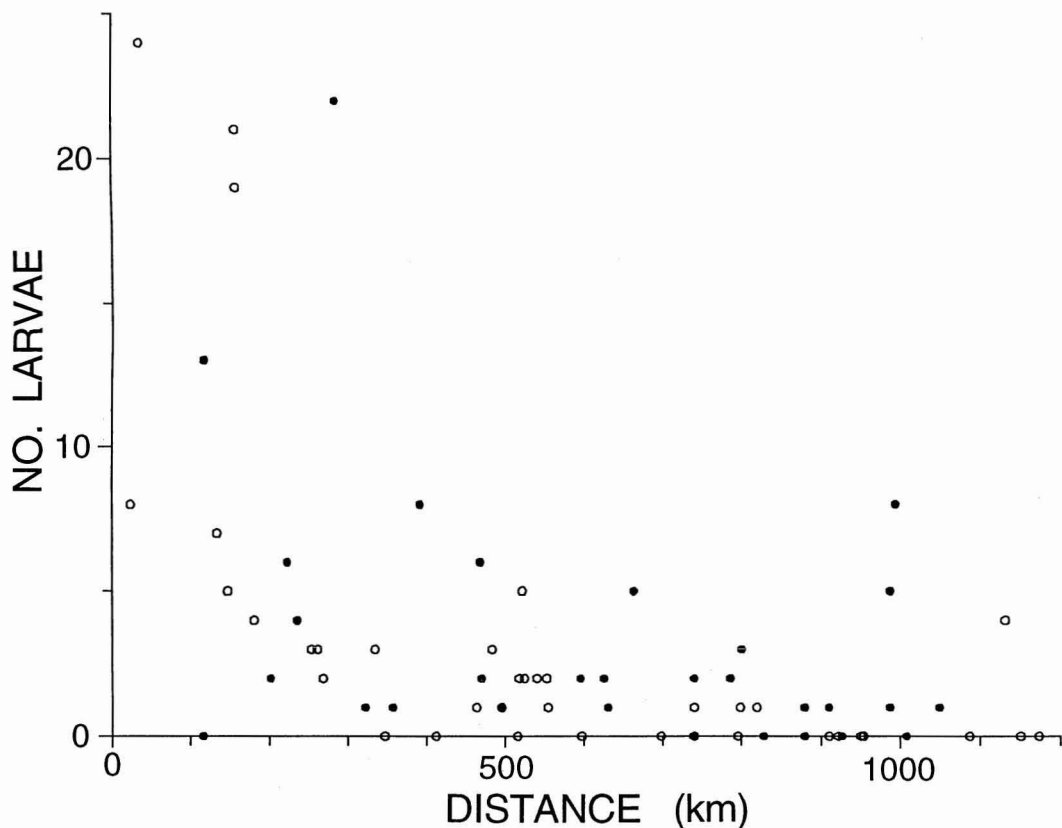


FIGURE 2. Number of nearshore fish larvae captured versus distance from the nearest island for 68 nighttime mid-water trawl samples taken in the central equatorial Pacific. Samples taken at latitudes of strong eastward currents ( $5-8^{\circ}$  N and  $2^{\circ}$  S- $2^{\circ}$  N) are indicated by solid circles, others by open circles. Data are from only those stations closest to small isolated islands; data from three other samples taken close to either the Hawaiian or Society islands have been omitted (see text).

nearest island, and 10 more only within 300 km. Included in these were *Parapercis* and Labrid S, the two most abundant taxa in Clarke's (1991) samples from ca. 13 km off Hawai'i, and families such as Gobiidae and Synodontidae, which were important in the latter samples. Larvae of *Parapercis*, Synodontidae, and Gobiidae were also found primarily very close to shore at Johnston Atoll by Boehlert et al. (1992). These results imply that larvae of most of the 38 "inshore" taxa rarely occur at extreme distances from the nearest adult populations.

Twenty-five taxa were taken at only one or two stations >300 km offshore. Nine of these were also taken more than twice in-

shore: Congrinae, Scorpaeninae, Apogoninae, Carangidae, Pomacanthidae, *Synagrops*, *Acanthurus*, *Ctenochaetus*, and *Bothus*. The offshore captures of the scorpaenine, one *Synagrops*, both *Acanthurus*, and both *Ctenochaetus* were downstream of Palmyra/Kingman ( $5-8^{\circ}$  N,  $150^{\circ}$  W), and those of one *Synagrops* and one *Bothus* were near the equator and downstream of Jarvis. The offshore captures of the congrine (*Rhechias*) and the pomacanthid were near  $15^{\circ}$  N,  $158^{\circ}$  W, conceivably within the range of transport by eddies from Hawai'i. Most of these taxa were regularly taken close to shore by Clarke (1991). (Eel and flatfish larvae were not covered in the latter report, but my unpublished



data indicate that larvae of congrines and *Bothus* were frequently present in the samples considered.)

Sixteen taxa taken only once or twice offshore were not taken frequently inshore either. Nine (Muraenosocidae, Ophidiidae, Lethrinidae, Epinephelinae, Echeneidae, Balistidae, *Plagiotremus*, Diodontidae, and *Pelecanichthys*) were not taken near shore, and seven (Holocentrinae, *Decapturus*, Chaetodontidae, Cirrhitidae, Labrid N, Ammodytidae, and Callionymidae) were represented by only one or two inshore captures. Seven of the 18 offshore larvae in these groups were taken at 5–8° N and four at 2° S–2° N. Except for *Decapturus*, which is a coastal pelagic species, and Callionymidae, larvae of none of these taxa appear to be particularly common even in waters close to shore (e.g., Clarke 1991, Boehlert et al. 1992).

Larvae of the setarchine scorpaenid *Ectreposebastes* (presumably *E. imus* Garman) were one of the most frequently taken taxa, and most (13/20) were taken >300 km offshore. Though adults occur in fairly deep water, they appear to be island-associated (Struhsaker 1973). Moser et al. (1977), however, reported larvae from 100 to 130° W along the equator—far from either South America or the central Pacific islands. Only seven of the 13 individuals taken offshore in the study reported here were from either near the equator or 5–8° N (i.e., directly downstream of likely nearshore sources), and one specimen, only 5.5 mm long, was from 18.4° N, 150° W—>500 km east and upstream of the island of Hawai'i. Thus at least some of the offshore captures probably resulted from offshore reproduction. Inclusion of *Ectreposebastes* larvae, however, had little effect on the overall trends considered above.

Eight other taxa were represented by more than two offshore captures. Of these, Mullidae were taken only offshore. One was from 7.9° N, 150° W and downstream of Kingman/Palmyra, and the others were from 10.3 and 11.5° N—north of the ECC and too far south to invoke transport by eddies from Hawai'i. Pseudogrammididae were taken only once inshore. The inshore capture and three of the offshore captures were from downstream of Jarvis; one offshore capture was

downstream of Palmyra/Kingman. Muræenids were taken in about equal numbers inshore and offshore, and *Luzonichthys*, Anthiinae (most were probably *Anthias*), Labrid T, *Chromis*, and *Naso* more frequently inshore than offshore. For the last six taxa, 22 of the 28 offshore captures were downstream of either Palmyra/Kingman or Jarvis. In none of these six taxa were there any obvious differences in size composition between inshore and offshore catches.

Overall, the results indicate that larvae of most taxa of nearshore fishes usually occur within 300 km of the nearest source and that most, but not all, captures at >300 km are associated with meso- or larger scale physical transport mechanisms (i.e., strong currents or eddies). Though densities of nearshore fish larvae at distances >300 km from shore are ca. 100 times lower than densities of most taxa close to shore (Clarke 1991), the offshore densities of nearshore larvae in the ECC and EUC are still equivalent to ca. 5000 larvae per square kilometer in terms of surface area. Given the horizontal extent, depth, and prevailing current velocities of the ECC and EUC above 100 m depth (Wyrski and Kilonisky 1982), roughly  $10^5$ – $10^6$  nearshore larvae are transported eastward across 150° W every day. That eastward "leakage" from the Line Islands postulated by Leis (1983) is this high is not surprising because Leis also calculated that passive transport from the Line Islands to ca. 150° W would take only ca. 20 days—less than the larval life span of the great majority of nearshore fishes.

One of the main reasons that so few nearshore larvae have been reported from offshore areas is that most ichthyoplankton surveys have sampled only a few hundred to a thousand cubic meters per tow with relatively small, slow nets. I previously pointed out (Clarke 1991) that such tows are insufficient for sampling many taxa even in waters close to adult populations. Because of the much lower densities estimated for offshore areas, not only is the probability of encountering even a single nearshore larva very low, but, as Leis (1984) pointed out, most larvae dispersed this far would be large enough to avoid most plankton nets. Further sampling with large, fast nets is needed to



confirm trends in the data reported here and could provide direct evidence of dispersal of larvae to even greater distances than shown here.

#### ACKNOWLEDGMENTS

I thank B. Mundy for assistance in identifying certain larvae.

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